Effects of water stress on *Haloxylon ammodendron* seedlings in the desert region of Heihe inland river watershed, Gansu Province, China

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Abstract: The water relation and leaf gas exchange of saxoul (*Haloxylon Ammodendron* Bge, a C_4 shrub) seedlings were studied under water stress in 2001. Saxoul seedlings maintained high transpiration when the soil moisture was above 11%. The seedlings were able to take up water from soil with above 6 % soil water content, which was the threshold level of soil moisture for seedlings. The relationship between transpiration and potential evaporation was linear for well-watered seedlings. The decrease of soil water availability led to different degrees of down-regulation of stomatal conductance, leaf transpiration and net CO_2 assimilation rate. The stomata played a relatively small part in determining the net CO_2 assimilation rate for the same seedling. The relationship between net CO_2 assimilation rate and transpiration was linear diurnally, and reduction scale of leaf transpiration was much bigger than that of net CO_2 assimilation rate by waters tress treatments, therefore intrinsic water-use-efficiency increased. High evaporative demand increased the leaf transpiration but inhibited net CO_2 assimilation rate. Because of the effect of VPD on transpiration in this region, the transpiration of well-watered and mild water stress seedlings becomes responsive to change in stomatal conductance over a wider range.

Keywords: *Haloxylon ammodendron,* Water stress; Leaf gas exchange; Water relation; Stomatal conductance; Seedling

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Introduction

Drought is known to limit plant survivorship and productivity in many regions especially in the arid regions of the world. Water stress is a limiting factor for a wide range of physiological processes in plants (Passioura 1988; Grantz 1990; Cornic 1994; Ben Haj Salah &Tardieu 1996; McDonald & Davies 1996; Seneweera *et al.* 1998). In the desert areas, the occurrence of shrubs and the amount of growth are controlled by the water supply. Water and, in particular, the shortage of water will have a dramatic impact on functioning and survival of shrubs. In response to water stress, plants regulate their transpiration by decreasing their stomatal conductance. The prime role of stomata might be avoided damaging plant through controlling water loss from plant, at same time, allowing photosynthesis. As water supply capability becomes threatened, stomatal regulation will insure that water use will not exceed supply (Sperry 2000). Many studies have shown that growth rates of several plants are directly proportional to the availability of water in the soil (Zhang 1989; Kramel and Loser 1995).

The present study was undertaken for a native and sand-fixed shrub species--saxoul (*Haloxylon ammodendron* Bge) that have formed a unique eco-geographical landscape in the desert areas of Heihe inland river watershed, Gansu Province, China. Saxoul is a C_4 shrub, which has widespread adaptability and can tolerate drought, impoverished soil and sand burial, and is one of the best sand-binding species in this region. Its main roots generally could extend over 10 m to reach the groundwater. Thirty years ago, a large area of trees and shrubs including saxoul were planted in the desert areas of Heihe inland river watershed, Gansu Province, where an average annual precipitation was 113.8 mm, 65% of which occurs from July to September. The scrub formed by saxoul has an important ecological role by protecting fragile sand soils from wind erosion, holding back moving sand. However, because of influences from human activities, the level of underground water table declined, which caused the low soil moisture in the soil depth 0-200 cm (Liu *et al.* 2002) and threatened the growth and survivorship of saxoul in this region.

Regeneration is essential to sustain populations of saxoul. Because the seedlings of saxoul are especially vulnerable to water stress, and germination and recruitment are thought to be critical stages in the life cycles. Seedling survival depends on adequate post-germination rainfall (Steenbergh & Lowe 1969; Jordaan & Nobel, 1982; Castellanos & Molina 1990; Esler and Phillips 1994). Through the investigation from 1997 to 2001, we did not find natural regeneration shrubs in saxoul stand in this region even though some saxoul seeds generated in May 1998 after a daily 22 mm rainfall event. The seedlings only survived less

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than 3 months and died from shortage of soil water in three 4x5 m^2 experimental plots. There is a growing interest in developing techniques for regeneration of saxoul. A better understanding of plant adaptation to water stress may help to regenerate saxoul and to enhance management practices. However, little information exists about the influence of water stress on physiological as well as the mechanisms to withstand water stress in saxoul. Large differences in water use between species can be attributed in part to differences in their 'hydraulic equipment' that is presumably optimized for drawing water from a particular temporal and spatial niche in the soil environment (Sperry *et al.* 2002). This study described the base question of relationship between seedlings and water.

Materials and methods

Plant materials

The experiment was carried out in the northern part of the Linze county at southwestern margin of the Badain Jaran desert between longitude 99°25'-100°25' E and latitude 39°4'-39°24' N during 2001. The study area belongs to desert climate, with an annual mean precipitation of 113.8 mm, annual evaporation 2 388 mm and annual mean air temperature 7.6 °C. Winds from northwest are dominant in the region, annual mean wind velocity is 3.2 $m \cdot s^{-1}$, maximum wind velocity 21 $m \cdot s^{-1}$, and annual days with wind of over velocity of 12 $m \cdot s^{-1}$ is 15 days. The depth of ground water is 2-5 m. Zonal soil is gray-brown desert soil.

Twenty saxoul seedlings were planted outdoors in 15 L containers filled with silt loam soil without draining. To avoid excessive soil temperature, the pots were placed in holes in the ground. One-year old seedlings with same appearance and root system were used. The twenty seedlings were transplanted to containers on the 8th May 2001. Prior to the water stress experiments, seedlings were well watered for 15 weeks and subjected to ambient conditions. Water stress treatments began on 25th August and ended on 13th September 2001. Of twenty seedlings, twelve seedlings selected, with same appearance, were watered with different water amounts, and different soil moistures were created at the beginning of water stress treatments, and then remained un-watered throughout the drying treatments, while the other eight seedlings had no water stress. In order to monitor the development of water stress, a balance with an accuracy to 1 g was used for monitoring soil moisture and evaportranspiration loss daily or hourly during the course of the water stress experiments. Pot and dry soil weight were recorded at the beginning of the experiment. This enabled us to determine gravimetrically the percentage water content of each pot. An evaporation pan placed on the study site allowed measurements of evaporation at the same time. At the end of the experiment, the seedling of each treatment was removed from the containers, and the dry weight of the total leaf, stems and roots were determined. Dry weight was determined after the material was dried in an oven at 60 °C for 72 h and the dried in an oven at 60 °C for 72 h and the ratio of dry weight and fresh weight were calculated.

Measurement of gas exchange

Gas exchange was measured with a portable open photosynthesis system LI-6400 (Li-Cor, Lincoln, NE, USA).

Results

Plant growth

The root and shoot mass of seedlings had a little differences due to shorter periods of water stress and the fresh weight and dry weight of leaf, stem and root also did not have significant differences between the treatments because the soil moistures were same for all the treatments in the end. The average values were shown in Table 1. The total dry weight of plant was not significantly reduced by water stress, with the exception of a bit color change of few leaves at the end of treatments, as compared with well-watered seedlings.

Table 1. Growth and morphological parameters of saxoul seedlings after treatments (each value is the mean of 6 seedlings)

Items	Fresh weight /g	Dry weight /g	Ratio of dry and fresh weights / %
Leaf	68.1±3.4	21.7±1.6	31.8±1.8
Stem	36.7±1.1	26.5±1.4	72.2±2.1
Root		20.4±1.6	
Total		68.5±3.8	

Status of soil water and environmental conditions

The soil moistures in six containers for water stress treatments were shown in Fig.1 including 3 raining days (2nd, 8th, 13th) when the soil moistures were increased. At the beginning of treatments, the maximum and minimum values of soil moisture were 20.65% and 11.15%, respectively. At the end of treatments, the soil moisture in different treatments was 6.4±0.32%, which was no significant difference.

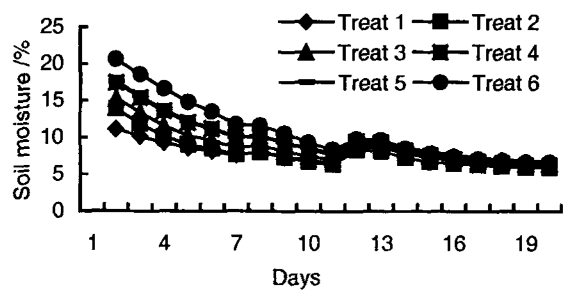

Fig. 1 The soil moistures in six containers for water stress treatments

The diurnal courses of photosynthetic photon flux density (PPFD), leaf–to–air vapour pressure deficit (VPD) and temperatures of leaf and air in the day of measuring gas exchange were shown in Fig.2. PPFD, VPD and tempera-

tures of leaf and air rose gradually until 14:00 hour. The maximum values of PPFD, VPD and leaf temperature were 1 733 μmol·m^{-2}·s^{-1}, 5.06 kPa and 34.4 °C, respectively at 14:00 hours. The PPFD at 18:00 hours reduced dramatically, but the temperatures of air and leaf and VPD reduced gradually after 14:00 hours. The difference of temperatures between air and leaf was less than 1°C. There was no difference in diurnal courses of PPFD, VPD and the temperatures of leaf and air between different seedlings.

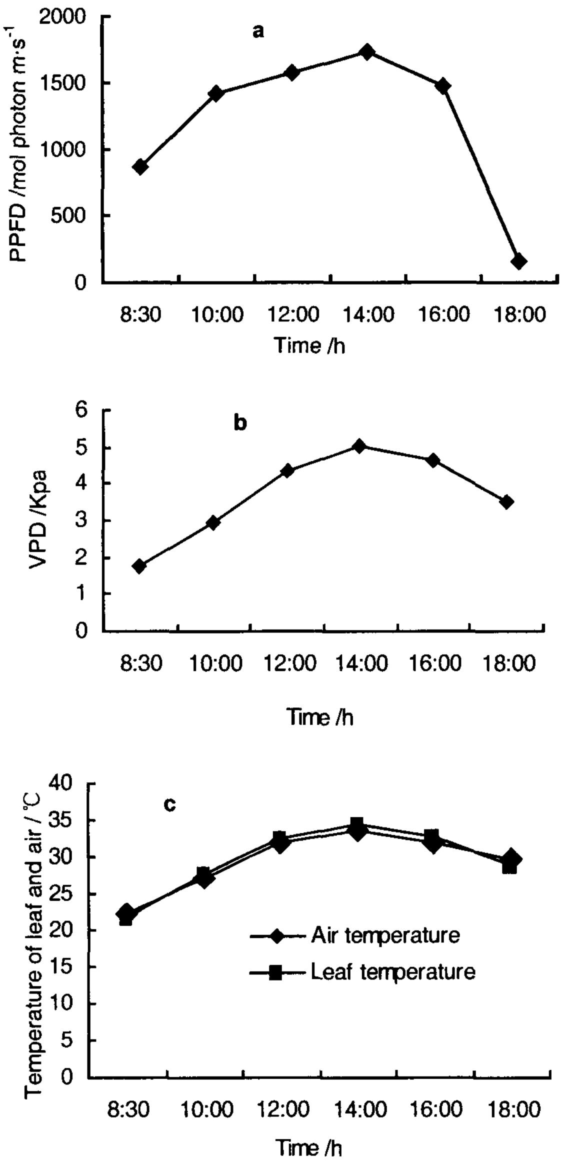

Fig. 2 Diurnal time courses of: photosynthetic photon flux density (PPFD) incident over a horizontal surface (a); leaf – to –air vapour pressure deficit (VPD), (b); temperatures of leaf and air (c). Data are average of 4 measurements

Water use of seedlings under water stress

The total evaportranspiration in six containers under water stress was separately 1.674, 2.319, 2.498, 3.074, 2.968 and 3.747 kg, during 16 days of drying treatment (excluding the raining days and the first day of treatments). At the end of treatments, the soil moistures were same. It means that the more water there was in the soil at the beginning, the more water the seedlings used under water stress conditions. The seedlings did not take up soil water when the soil moisture was below 6%, which was the threshold level of soil moisture for seedlings.

The relationships between potential evaporation and transpiration for hourly and daily under well-watered condition were linear and shown in Fig. 3. We used the daily equation (y=21.085x+29.468, R^2=0.89) and potential evaporation to calculate the transpiration of seedlings per day under well-watered condition for 16 days of drying. Total transpiration was 2.661 kg. If the actual evportranspirations of seedlings determined by weighting the six containers everyday were divided by 2.661 kg, the ratios were 62.9%, 87.1%, 93.9%, 116%, 112% and 141% separately which means that the 3 seedlings would not have suffered from water stress if they had used all the soil water for transpiration. However, if the actual evaportranpirations per day minus the transpirations multiplying their ratios (the results were shown in Fig.4), we found that all the seedlings were stressed by shortage of water during the half of total experiment days. More than half supplied water was evaporated through soil without being used by seedlings.

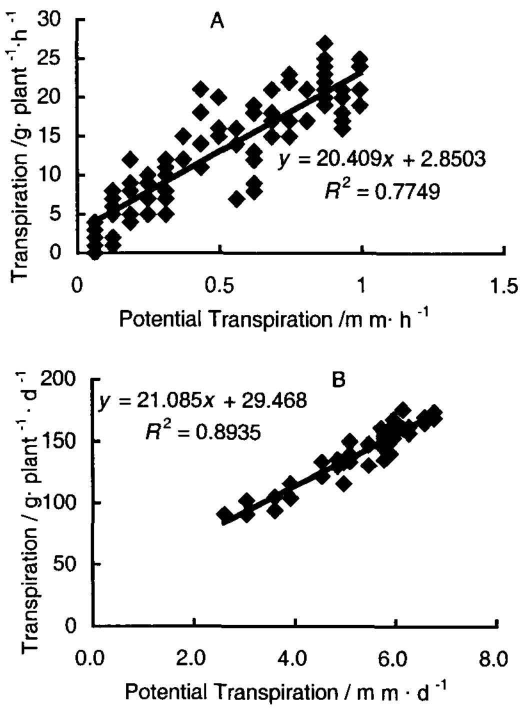

Fig.3 The relationships between potential evaporation and transpiration of saxoul seedlings for hourly (A) and daily (B) under well-watered condition

Gas exchange

When we measured the transpiration of seedlings, we found that the transpiration did not reduce if the soil moisture was above 11%. Therefore, four seedlings whose soil moisture was separately 18.2 % (1 well-watered seedling), 8%-10% (2 mild water stress seedlings) and 6.9% (1 se-

vere water stress seedling) were selected and their gas exchange patterns were determined. The diurnal patterns of gas exchange were clearly different in different seedlings that had different soil water moisture on 4th August 2001 although the other conditions were same. The net photosynthetic rate increased gradually in the morning and peaked approximately at 16:00 hours (Fig. 5). The maximum photosynthetic rate was reduced by the decline of the soil moisture or water stress conditions. Leaf conductance was at a maximum at 08:30-10:00 hrs, decreased gradually until 12:00 hours. However, the leaf conductance of seedlings under severe water stress had the minimum value (13.0 mmol H_2O $m^{-2}\cdot s^{-1}$) at 12:00 and 18:00 hours. The transpiration rate peaked at 12:00 hours in well-watered and mild water stress seedlings, but contrary to expectation it was very interesting to find that the transpiration rate of seedlings under severe water stress at 12:00 hours was its second lowest value. Transpiration rate always reduced as soil moisture decreased. The relationship between net CO_2 assimilation rate and leaf transpiration for all seedlings was linear (Fig .6). Hence, this pattern suggests that the net CO_2 assimilation rate and leaf transpiration were related to soil water availability.

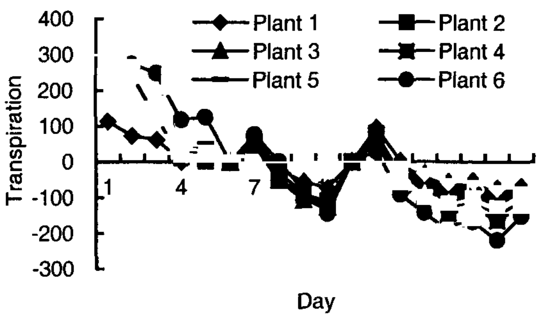

Fig.4 Curve of actual evaportranpirations of saxoul seedlings per day minus the transpirations multiplying their ratios

The averages of net CO_2 assimilation rate), stomatal conductance) and leaf transpiration) for water stress seedlings declined due to the water stress (Table 2). Although a reduction in all parameters was imposed by three waters tress treatments, the reduction of leaf transpiration was much higher than that of net CO_2 assimilation rate, and therefore intrinsic water-use-efficiency increased.

Discussion

Saxoul seedlings maintained high transpiration when the soil moisture was above 11%. The seedlings were able to take up water from soil with above 6% soil water content, which was the threshold level of soil moisture for seedlings. The relationship between transpiration and potential evaporation is linear. These features are thought to contrast with the relatively low transpiration rates and gradual stomatal closure in drought-tolerant seedlings in response to soil drying.

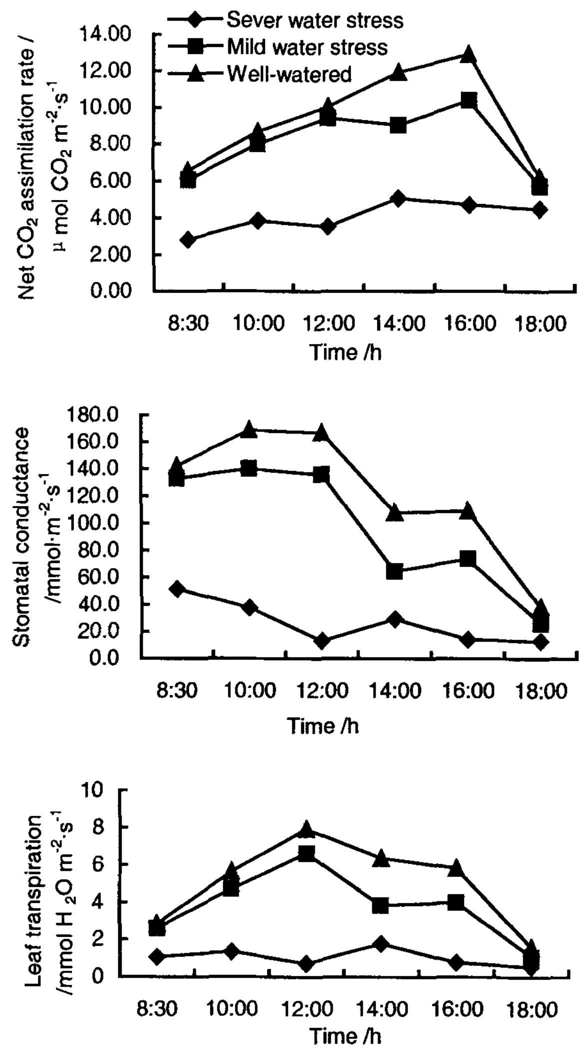

Fig.5 The diurnal patterns of gas exchange in different seedlings of saxoul and different soil water moistures on August 4, 2001

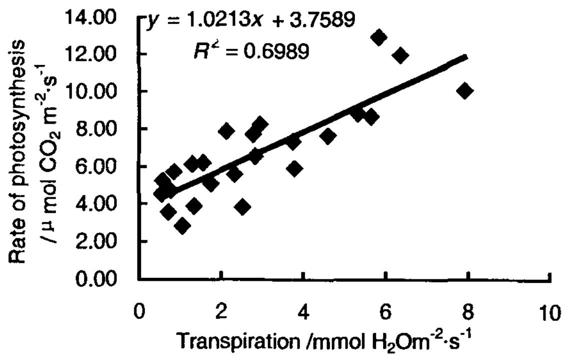

Fig.6 Correlation between photosynthesis (μmol CO_2 $m^{-2}\cdot s^{-1}$) and transpiration (mmol H_2O $m^{-2}\cdot s^{-1}$)

Values are from well-watered, mild water stress and sever water stress seedlings.

According to our field observations, the early stage of growth of saxoul seedling is an important bottleneck for the survivorship of seedling in this areas, because the rainfall does not significantly influence the soil water storage of

stand in 0-200 cm where there has very low soil water content, which means that the most rainfall of a month was completely consumed by evapotranspiration and seepage at the same time (Liu *et al.* 2002). Therefore, if one wished to regenerate this species, supplement irrigation would have to be provided at the early seedling stage. In our experiment, since more than half amount of water was evaporated from soil surface, and we must take some measures to prevent soil evaporation in the field conditions. At the same time, it is necessary to develop techniques that can make seedlings extending their root system to groundwater as early as possible.

Table 2. Daily average net CO_2 assimilation rate, stomatal conductance, leaf transpiration and intrinsic water-use-efficiency (net CO_2 assimilation rate / leaf transpiration of well-watered, mild water stress and severe water stress seedlings

Treatments	Net CO_2 assimilation rate /μmol CO_2 $m^{-2}\cdot s^{-1}$	Stomatal conductance /mmol H_2O $m^{-2}\cdot s^{-1}$	Leaf transpiration/mmol H_2O $m^{-2}\cdot s^{-1}$	Net CO_2 assimilation rate / leaf transpiration
Ww	9.40	122 18	5.03	1.87
Mw	8.12	95.62	3.80	2 13
Mw/Ww /%	86.4	78.3	75.6	114.2
Sw	4.10	26.43	1.04	3 95
Sw/Ww /%	43.6	21.6	20.6	211.6

Ww: Well-watered seedlings, Mw: Mild water stress seedlings, Sw: Severe water stress seedlings

The responses of the treated seedlings to net CO_2 assimilation rate, stomatal conductance and leaf transpiration showed that water stress strongly affect the leaves of seedlings. These indexes were closely related to soil water status (Fig.5). The stomata played a relatively small part in determining the rate of photosynthesis for the same seedling because the photosynthesis increased while the stomata conductance decreased. The relationship between photosynthesis and transpiration was linear daily, and the reduction scale of leaf transpiration was much bigger than that of the net CO_2 assimilation rate by waters tress treatments, therefore intrinsic water-use-efficiency increased. Water played a key role for seedlings survivorship and growth in this arid region. High evaporative demand increased the leaf transpiration, and inhibited net CO_2 assimilation rate (Fig.5). Due to the alleviation of the negative effect of high evaporative demands on net CO_2 assimilation rate when the evaporative demand was relative low, net CO_2 assimilation rate was increased under conditions of lower leaf transpiration and stomatal conductance. Because of the effect of VPD on transpiration in this region, the transpiration of well-watered and mild water stress seedlings becomes responsive to change in stomatal conductance over a wider range. We also found that the stomatal conductance changes with evaporative demand. The stomata conductance decreased in 1-2 hours during middle days. However, the stomatal of sever water stress seedling closed and reopened earlier than that of well-watered and mild water stress seedlings (Fig.5). The function of stomata in our case was a buffer of reducing water loss from leaves of same seedling.

The water relations of seedlings strongly influenced its growth and development in water-limited environments. An understanding of seedling responses to water scarcity provide some insight into restoration management problems (Esler *et al.* 1994). Very few literatures reported the performance of saxoul seedlings in the desert region of Heihe river watershed. This studies addressed the water relations of saxoul seedlings in water-limited environments, which would guide research, identify the need for new measurements, and evaluate the relationship among multiple processes that ultimately contribute to plant regeneration, growth and development in the desert environment. However, this needs more information and investigation.

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